TITLE:

Developmental changes in feeding behaviors of infant chimpanzees at Mahale, Tanzania: Implications for nutritional independence long before cessation of nipple contact

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CITATION:

Matsumoto, Takuya. Developmental changes in feeding behaviors of infant chimpanzees at Mahale, Tanzania: Implications for nutritional independence long before cessation of nipple contact. American Journal of Physical Anthropology 2017, 163(2): 356-366

ISSUE DATE:

2017-06

URL:

http://hdl.handle.net/2433/225122

RIGHT:

This is the peer reviewed version of the following article: Matsumoto T. Developmental changesin feeding behaviors of infant chimpanzees at Mahale, Tanzania:Implications for nutritional independence long before cessationof nipple contact . Am J Phys Anthropol. Volume 163, Issue 2 (2017-06);163:356–366.https://doi.org/10.1002/ajpa.23212, which has been published in final form at https://doi.org/10.1002/ajpa.23212. This article may be used for non-commercial purposes in accordance with Wiley Terms and Conditions for Self-Archiving."; 許諾条件により本文は2018-05-19に公開; この論文は出版社版でありません。引用の際には出版社版をご確認ご利用ください。; This is not the published version. Please cite only the published version.

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Title

Developmental changes in feeding behaviors of infant chimpanzees at Mahale, Tanzania: implications for nutritional independence long before cessation of nipple contact

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Keywords

weaning, food transfer, M1 eruption, life history variable, dietary transition

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Number of text pages: 34

Number of figures: 2

Number of tables: 2

Abbreviated title

Feeding behavioral changes in infant chimpanzees

Grant sponsorship

This research was financially supported by the Ministry of Education, Culture, Sports, Science, and Technology (MEXT) KAKENHI (Grant number 19255008, 19107007, 24255010); and Japan Society for the Promotion of Science (JSPS) KAKENHI (Grant number 14J00562, 16J03218).

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Abstract

Objectives: Weaning of chimpanzees is considered to occur at 4–5-years-old with complete cessation of nipple contact and timing of reconception calculated by inter-birth interval minus gestation length. This is also the basis of "early weaning" in humans (i.e., approximately 2.5-years-old). However, recent studies of the survival of orphans and the first molar (M1) eruption in wild chimpanzees have predicted that infants move towards nutritional independence at 3-years-old. Therefore, this study aimed to investigate ontogeny of feeding behavior at around 3-years-old in wild infant chimpanzees.

Materials and Methods: I studied 19 infants aged 1–60 months in the M group in Mahale Mountains National Park, Tanzania. The total observation time was 518 hours, 25 minutes.

Results: At around 3-years-old, infant chimpanzees spent more total feeding time, and time feeding on leaves, and food physically difficult to process without food transfer from other individuals. These results suggest that infant chimpanzees significantly reduced their dependence on milk for nutrition at around 3-years-old, that is, before cessation of nipple contact.

Discussion: This study suggests that M1 eruption in wild Eastern Chimpanzees is an index of the period when infants move towards nutritional independence with a key dietary transition. This is the first study to provide behavioral evidence of the large temporal gap between nutritional independence of infants and reconception of mothers in great apes, and clarify the unique feature of human life history whereby mothers can reconceive before an infant reaches nutritional independence.

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Introduction

Recent studies have attempted to reveal the unique features of human life history by comparing life history parameters, such as lifetime reproductive success, inter-birth interval, and weaning age, between primate species (Bogin, 1999; Duda and Zrzavý, 2013; Meehan and Crittenden, 2016). Researchers propose that one of the most important features of human life history is early weaning (Humphrey, 2010), supported by prepared complementary foods by the mother and allo-mothers to meet the nutritional requirements of infants (Humphrey, 2010; van Noordwijk et al., 2013a). Sellen (2001) suggested a human weaning age of approximately 2.5-years-old (ranging from 0.5 to 8 years), based on data from questionnaires about cessation of breastfeeding in 113 modern nonindustrial populations. The typical weaning age of archaeological populations estimated by recent studies using stable isotopes was approximately 2.5−3-years-old, indicating it is similar to that of modern nonindustrial populations, even though there are large variations (Tsutaya and Yoneda 2013; Tsutaya et al. 2016). In addition, research on the distribution of barium in teeth indicated that the weaning age of Neanderthals was 1.2-years-old (Austin et al., 2013).

Conversely, the weaning age of wild non-human primates is generally estimated by complete cessation of nipple contact as a behavioral index of nursing (Machanda et al., 2015). Chimpanzees (*Pan troglodytes*), the species genetically closest to humans, have been observed to continue nipple contact until 4−5-years-old (e.g., Goodall, 1986). This period matches the timing of conception of the next offspring, which is calculated using the birth date of the next offspring minus gestation length (Emery Thompson et al., 2007; Emery Thompson, 2013; Lee et al., 1991). Therefore, demographic studies of chimpanzees usually assume that the age at which

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73 infants are weaned is 4–5-years-old (Goodall, 1986; Hiraiwa-Hasegawa et al., 1984; Nishida et al., 1990).
74 Compared to chimpanzees (4−5-years-old), earlier weaning in humans (2.5−3-years-old) is related to other
75 features of human life history, such as a shorter inter-birth interval and higher lifetime reproductive success
76 (Humphrey, 2010).

77 However, it should be pointed out that weaning is not a simple event, but is a process that begins with the
78 onset of solid food intake (Humphrey, 2010; Langer 2008; Lee, 1996; van Noordwijk et al., 2013a). The end of
79 the weaning process of infants is defined as the period when infants are independent of maternal milk for
80 nutrition (Lee, 1996). Consequently, anthropological studies have investigated the weaning age based on the
81 termination of maternal milk provisioning (Sellen, 2007). Yet, many behavioral studies of nonhuman primates,
82 especially those of wild populations, regard nipple contact as a good measure of actual nursing because this
83 behavior is easy to observe, even in wild (e.g., Tarnaud, 2004). However, it is difficult to identify the end of
84 weaning based on the complete cessation of nipple contacts for two reasons. First, some infants, including
85 chimpanzees, suckle without receiving milk (Bădescu et al., 2016; Nishida, 1994; Tanaka, 1992). Bădescu et al.
86 (2016) confirmed the occurrence of suckling without milk transfer (i.e. comfort nursing) by analyzing the stable
87 isotopes in the feces of wild chimpanzees. Second, nursing might occur at night, when direct observations are
88 not usually conducted. Using fecal stable isotopes, Reitsema (2012) suggested that Francois' langur
89 (*Trachypithecus francoisi*) nurses at night. Therefore, complete cessation of nipple contact may not be a suitable
90 index of the period when infants become nutritionally independent of maternal milk.

91 An alternative index of nutritional independence in wild populations is the earliest age at which orphans with

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92 adoptive mothers can survive without nursing. Boesch et al. (2010) reported that the earliest age of orphan
93 chimpanzees adopted by a non-mother without nursing and surviving for more than two years in Taï, Côte
94 d'Ivoire, was 30-months-old. In Mahale, two orphans of 37-months-old survived for more than two years without
95 nursing, but those less than 29-months-old did not survive (Nakamura and Hosaka, 2015; Mahale Mountains
96 Chimpanzee Research Project, unpublished data). In addition, orphans brought to sanctuaries before 2–3 years
97 of age rarely survive (Wobber and Hare, 2011). These studies suggest that chimpanzees significantly reduce
98 their dependence on milk for nutrition at around 3-years-old. From here on, the point at which infants
99 considerably reduce dependence on maternal milk for nutrition is termed "nutritional independence", based on
100 Borries et al. (2014).

101 The first molar (M1) eruption coincides with the timing of weaning in many primates and, therefore,
102 considered a "morphological landmark of independence for primates" (Smith, 1992). However, discordance
103 between M1 eruption and weaning age is observed among the great apes (Robson and Wood, 2008), although
104 "weaning age" is determined in this case by cessation of nipple contact, which as aforementioned may not be a
105 suitable index. Recent studies revealed that M1 eruption in wild chimpanzees in Kanyawara, Uganda, occurs at
106 approximately 3-years-old (30–40-months-old) (Machanda et al., 2015; Smith et al., 2013), which is similar to
107 the earliest age of survival potential of adopted orphans (Smith et al., 2013).

108 Stable nitrogen isotope analysis of dentine serial sections of wild chimpanzees suggested that maternal milk
109 transfer decreases gradually after 1–2-years-old of age (Bădescu et al., 2016; Fahy et al., 2013). However,
110 another study suggested that maternal lactation effort remains stable throughout infancy, due to their multi-year

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111 lactation capacity (van Noordwijk et al., 2013a). In either case, the weight and height of infants continues to
112 increase (Hamada and Udono, 2002), requiring supplementation with food, other than milk, to meet their
113 nutritional needs (Hinde and Milligan, 2011). As aforementioned, recent studies on orphans and M1 eruption
114 suggest that infant chimpanzees at 3-years-old considerably reduced dependence on maternal milk earlier than
115 the existing weaning age. If this is indeed the case, then important changes in feeding behavior of infants before
116 and after age 3 would be expected. In non-human primates, infants move towards nutritional independence by
117 selecting suitable solid food from a variety of options in their environment (Galef, 2009). However, before
118 achieving nutritional independence, infants encounter several aspects of difficulty in feeding due to immaturity
119 (Altmann, 1980). For example, infants are unable to digest food containing large quantities of fiber and
120 secondary compounds, especially leaves, due to the immaturity of their digestive organs and small body mass
121 (Agetsuma, 2001; Hiraiwa-Hasegawa, 1990a; Nowell and Fletcher, 2008). Since leaves are important protein
122 sources for chimpanzees (Nishida, 2012; Takemoto, 2003), and protein in milk is necessary for development of
123 body mass in apes (Hinde and Milligan, 2011), infants are expected to become able to feed on and digest leaves
124 at the point when infants move towards nutritional independence. Additionally, infants cannot process and eat
125 food that is physically difficult to process (e.g., fruits covered with a hard shell), as they lack the processing
126 skills and physical strength (Nishida and Turner, 1996; Taniguchi, 2015). Although human infants confront
127 similar challenges, they become nutritionally independent earlier, due to the easily digestible (and nutritionally
128 rich) foods provided by caregivers (i.e. complementary foods) (Sellen, 2007). Infant chimpanzees can receive
129 physically difficult food to process from other individuals; however, these items are generally less nutritionally

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valuable as they are small and/or leftovers (Hiraiwa-Hasegawa, 1990c; Nishida and Turner, 1996; Silk, 1978). Therefore, it is considered important for infant chimpanzees to be able to process and eat such food without food transfer from other individuals.

This study investigated the ontogeny of feeding behavior in wild infant chimpanzees to examine whether nutritional independence is associated with changes in infant feeding behavior. Three predictions were tested: (1) Infants spend more time feeding at around 3-years-old, to accommodate an increased need for nutrition; (2) Infants spend more time feeding on leaves at around 3-years-old, to meet the increased need for protein; (3) Infants spend more time feeding on food physically difficult to process without food transfer from other individuals, as they become able to process physically difficult food by themselves to receive adequate nourishment. This study also investigated the ontogeny of nipple contact, which is the existing index of the weaning period, to validate the consistency of weaning age with previous studies.

Materials and Methods

The study periods were from January to September, 2011, from October 2012 to July 2013, and from June to August, 2015. The subjects were Eastern Chimpanzees (*Pan troglodytes schweinfurthii)* of the M group in Mahale Mountains National Park in Tanzania (6°15′ S, 29°55′ S) (Nakamura and Itoh, 2015). Individuals of the M group have been studied since 1965 and individually identified since 1980 (Hiraiwa-Hasegawa et al., 1984). The core area of chimpanzee habitat is the west side of Mahale Mountains between 780 and 1300 m a.s.l (Nakamura et al., 2013), consisting of mosaic patches of *Erythrophleum* forest and *Pycnanthus-Xylopia* forest,

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colonizing forest dominated by species such as *Senna spectabilis* and *Croton sylvaticus*, and woodland comprising *Combretum spp.*, Miombo (*Brachystegia bussei*) woodland, and swamp (Itoh and Nakamura, 2015b). In general, the dry season begins in early October and the wet season in mid-May (Itoh, 2015). Chimpanzees generally travel in fission-fusion grouping patterns to search for several species of fruits that vary seasonally (Itoh and Nakamura, 2015a; Norikoshi, 2002).

The permission to study wild chimpanzees in Mahale Mountains National Park was granted by the relevant governing bodies in Tanzania: the Tanzanian Commission for Science and Technology, the Tanzanian Wildlife Research Institute, and Tanzania National Parks (permit number 2010-215-NA-2009-26, 2011-166-ER-2006-26, 2012-409-ER-2009-26, and 2015-165-ER-2009-26).

I observed 19 infants aged 1–60 months using the focal animal sampling method (Altmann, 1974). I followed the target as far as I could, and recorded movements of infant mouths, including lip, mouth, bite, lick, and chew by continuous recording. I also recorded the target of the movement, and the start and end times. For infant mouth movements, I defined licking and/or chewing as feeding to exclude play feeding (Watts, 1985), which is not nutritionally valuable. End time of feeding was determined as the end time of licking and/or chewing. If infants started to play or travel continuously, end time was determined as the start of play or travel. I determined that feeding time continued when infants performed some mouth movements on the same target again within 30 seconds even though I was unable to observe mouth movements temporarily within 30 seconds. When the target was a plant, I recorded the plant part that was targeted, such as fruit, leaf, petiole, flower, seed, resin, pith, wood, or bark.

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168 Nipple contact time was also recorded. If an infant transitioned from nipple contact to ventro-ventral
169 movement with the mother while still suckling, I included the time of ventro-ventral movement as additional
170 nipple contact time. In addition, when an infant was in ventral contact with the mother and I could not observe
171 the mouth movements, if I was able to confirm nipple contact later (and the infant remained in ventral contact),
172 I included the period when the infant remain in ventral contact with the mother as additional nipple contact time.
173 Infant chimpanzees always travel with the mother, rarely venturing far alone (Hayaki, 1988). Therefore,
174 even if a food item is highly available in the environment, infants have little opportunity to eat it unless the
175 mother visits the food patch. Therefore, maternal feeding time might reflect the availability of a food item for
176 infants. I recorded the activity of the mother, including feeding and traveling by instantaneous sampling at 5-
177 min intervals (Altmann, 1974). When the mother fed on plants, I recorded the plant parts targeted as above.
178
179 *Data analysis*
180 One severely disabled infant was excluded from the analysis (see Matsumoto et al. (2016) for details). Total
181 observation time was 518 h, 25 min. I excluded observation time when I could not observe the mouth
182 movements of infants. Even though the mouth movements of infants could not be observed, I include the time
183 when there was no objects around infants' head and infants did not have or mouth anything before, as "not
184 feeding" time. Therefore, the total analysis time was 400 h, 45 min. I divided analysis time by individuals and
185 by days. For example, data from different individuals on the same day were considered as independent. A total
186 of 121 data points was analyzed. I calculated the age of infants in months by subtracting the month of the study

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187 from the month of first observation of the infant (see Table 1 for detailed information of subject individuals).

188 **[Table 1 here.]**

189 I determined the feeding time in which the food target was shared by other individuals and/or by food
190 transfer as feeding time with food transfer after Nishida and Turner (1996). I classified the target of feeding as
191 difficult food for infants to process using the list of difficult food and the definition given in Nishida and Turner
192 (1996). I excluded ant-fishing from the analysis of food physically difficult to process as previous studies have
193 already revealed that infants over 36-months-old start to ant-fish (Nishida and Hiraiwa, 1982; Nishie, 2011). I
194 did not observe infants feeding on meat during the current study though previous study reported that infants
195 spent 0.6 % of their feeding time on meat (Hiraiwa-Hasegawa, 1990a).

196 Continuous feeding time and nipple contact time were converted to scan points at 1-min intervals. Using
197 maternal data of scan points at 5-min intervals, I calculated the indexes as follows: maternal feeding time ratio
198 = no. of scan points for feeding/no. of total scan points; maternal traveling time ratio = no. of scan points for
199 traveling/no. of total scan points; maternal leaf feeding time ratio = no. of scan points for feeding on leaves/no.
200 of total scan points; maternal time ratio for feeding on food difficult to process = no. of scan points for feeding
201 on food difficult for infants to process /no. of total scan points.

202

203 **Statistical analysis**

204 I used Generalized Additive Mixed Models (GAMMs) to examine the influence of developmental changes
205 (age in months) on each feeding time and nipple contact time, as GAMMs fits smooth functions to non-linear

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206 data and uses random effects for repeated measures on the same subject. GAMMs have been used in previous
207 studies of ontogeny of behavior (e.g., chimpanzee development in Gombe; Lonsdorf et al., 2014). I used the
208 gamm4 package (Wood and Scheipl, 2015) in R 3.1.2 (R Core Team, 2015) and tested predictions by
209 constructing GAMMs with a binomial error distribution and a logit link function. I used Akaike's information
210 criterion for model selection (Burnham and Anderson, 2002), and selected the model with the smallest AIC
211 value and examined the model(s) that had a ΔAIC (AIC value difference from the best model) of <2 (Burnham
212 and Anderson, 2004). I checked multi-collinearity between explanatory variables using the DAAG package
213 (Maindonald et al., 2015). The variance inflation factors (VIF) were sufficiently low among variables of each
214 model (VIF <2).

215 Response variables and explanatory variables for each model are detailed below. Maternal feeding time ratio
216 (on all food items, leaves, and food physically difficult to process for infants) was included as an explanatory
217 variable for the index of availability of food items to infants. In addition, maternal traveling time ratio was also
218 added as an explanatory variable as the index of travel distance during the observation time.

219

220 (A) Nipple contact I used nipple contact time/total observation time of an infant as the response variable; age in
221 months (fit smooth function), maternal feeding time ratio, and maternal traveling time ratio as the explanatory
222 variables; and infant ID as random effects.

223 (B-1) Total feeding time I verified prediction (1), using feeding time/total observation time of an infant as the
224 response variable; age in months (fit smooth function), maternal feeding time ratio, and maternal traveling time

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ratio as explanatory variables; and infant ID as random effects.

(B-2) Feeding time on leaves I verified prediction (2), using feeding time on leaves/total observation time of an infant as the response variable; age in months (fit smooth function), maternal leaf feeding time ratio, and maternal traveling time ratio as explanatory variables; and infant ID as random effects.

(B-3) Food transfer I verified prediction (3) using feeding time on food physically difficult to process with food transfer/total feeding time on food physically difficult to process as the response variable; age in months (fit smooth function), maternal time ratio for feeding on food physically difficult to process, and maternal traveling time ratio as the explanatory variables; and infant ID as random effects.

When the influence of age in months on each response variable changed significantly, I estimated age in months to determine and evaluate the developmental change points. The number and value of the change points was determined by assuming smoothing splines as a combination of linear expressions (Crawley, 2005). Estimated change points are shown in Figure 2. The actual change points cannot be directly determined as smoothing splines cannot be differentiated; therefore, I analyzed the actual change points using generalized linear mix models (GLMMs). I used age and “age -age at the estimated change point” as explanatory variables in each model. This meant that summing of linear expressions, which change the coefficient at the point of estimated change point, approximates the smoothing spline (Crawley, 2005). I detected the actual change point ±3 months of the estimated change point, which showed the smallest AIC using GLMMs with a binomial error distribution and a logit link function. When there were multiple estimated change points, I examined the combination of change points that produced the smallest AIC in each model. I used the glmmML package

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244 (Bronstrom, 2013) for these analyses.

245

246 **Results**

247 Figure 1 [A] shows the ontogeny of nipple contact time. In the best model, age in months significantly
248 affected nipple contact time ratio ($P < 0.001$). The effect of maternal feeding time ratio was negative ($P < 0.01$)
249 and maternal traveling time ratio was non-significant ($P > 0.1$) (see Table 2 for details).

250 **[Table 2 here.]**

251 **[Figure 1 here.]**

252 Figure 2 [A] shows smoothing splines of age in months and the estimated change points in nipple contact
253 time. An actual change point in nipple contact was detected at 48-months-old in the GLMMs analysis. Nipple
254 contact time decreased gradually before 48-months-old, and started rapidly decreasing after 48 months. This
255 trend matched well with the weaning age using the conventional definition (cessation of nipple contact). An
256 obvious developmental change in nipple contact time, especially around 36-months-old, was not detected.

257 **[Figure 2 here.]**

258 Figure 1 [B-1] shows the ontogeny of total feeding time. In the best model, age in months significantly
259 affected feeding time ratio ($P < 0.001$). The effect of maternal feeding and traveling time ratio was positive and
260 negative, respectively (both $P < 0.01$) (see Table 2 for details). Change points in feeding times were detected at
261 10, 38, and 44-months-old (Fig. 2 [B-1]). Feeding time increased gradually before 3-years-old and increased
262 more rapidly after 3-years-old.

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263 Figure 1 [B-2] shows the ontogeny of feeding time on leaves. In the best model, age in months significantly
264 affected feeding time ratio ($P < 0.001$). The effect of maternal leaf feeding and traveling time ratio was positive
265 and negative, respectively (both $P < 0.01$) (see Table 2 for details). Change points in feeding times on leaves
266 were detected at 10, 29, and 36-months-old (Fig. 2 [B-2]). Infants between 29 and 36-months-old significantly
267 increased feeding time on leaves.
268 Figure 1 [B-3] shows the ontogeny of feeding time on food physically difficult to process with food transfer
269 in total feeding time on food physically difficult to process (food transfer ratio). In the best model, age in months
270 significantly affected food transfer ratio ($P < 0.001$). The effect of maternal time ratio for feeding on difficult
271 food to process was positive ($P < 0.01$) but maternal traveling time ratio was non-significant ($P > 0.5$) (see Table
272 2 for details). Change points in food transfer ratio were detected at 11 and 30-months-old (Fig. 2 [B-3]). Infants
273 over 30-months-old started to decrease food transfer ratio. Infants around 3-years-old showed a significant
274 decrease in food transfer ratio.
275
276 **Discussion**
277 The results supported the predictions (1), (2), and (3), and were consistent with the results of previous studies
278 that conclude a weaning age at 4−5-years-old using nipple contact as an index (Hiraiwa-Hasegawa, 1990b;
279 Matsumoto and Hayaki, 2015). However, major changes in feeding behavior at around 3-years-old confirmed
280 that infant chimpanzees significantly moved towards nutritional independence earlier than the “weaning age”
281 determined by the current index. Therefore, this study suggested that nutritional independence (i.e.,

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282 physiological weaning), when infants significantly reduce their dependence on maternal milk for nutrition,
283 occurs at 3-years-old, whereas nipple contact ceases at 4−5-years-old. This temporal gap between nutritional
284 independence and weaning age based on the cessation of nipple contact was also detected by a staple isotopic
285 analysis of chimpanzee feces in Ngogo, Uganda. However, age differed among groups (i.e., nutritional
286 independence and weaning age were at 4-years-old and 6 years old, respectively, in Ngogo) (Bădescu et al.,
287 2016).

288 A change point at 38-months-old was observed in ontogeny of feeding time. The smoothing spline of age in
289 months showed that feeding time increased gradually before 38-months-old and more rapidly after 38-months-
290 old. In other words, developmental changes in feeding time between the other two change points, i.e., 1−4-
291 years-old, did not increase linearly. This developmental change in feeding time at around 3-years-old was seen
292 in previous studies of development of chimpanzees at other field sites, such as Kibale (Smith et al., 2013) and
293 Gombe, Tanzania (Lonsdorf et al., 2014). Most infants over 36-months-old were able to ant-fish (Nishida and
294 Hiraiwa, 1982; Nishie, 2011). This shift would reflect the developmental changes in total feeding time at around
295 3-years-old.

296 Although infants younger than 29-months-old spent little time feeding on leaves, those aged 29−36 months
297 drastically increased their feeding time on leaves. Maturation of digestive organs and increasing body mass may
298 enable infants to eat more leaves, which contain much fiber and secondary compounds (Agetsuma, 2001;
299 Nowell and Fletcher, 2008). Hiriwa-Hasegawa (1990a) showed that infant chimpanzees spend more time than
300 adults feeding on young leaves that contain relatively lower fiber and secondary compounds. However, changes

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in the types of leaves targeted by infants were not investigated here, as it was not possible to discriminate leaf type. This study showed that drastic changes in feeding time on leaves between 29- and 36-months-old occurred just before the period when infants are assumed to move towards nutritional independence. Leaves provide a protein-rich diet (Nishida, 2012), and infant chimpanzees could compensate for the need of protein and be nutritionally independent after 36-months-old.

Infant chimpanzees older than 30-months tended to spend more time feeding on food difficult to process without food transfer; however, this time drastically decreased by the age of 36 months. Previous studies suggested that food gained by food transfer has low nutritional value (Hiraiwa-Hasegawa, 1990c; Nishida and Turner, 1996; Silk, 1978). Therefore, it is possible that infants older than 30-months-old can eat food physically difficult to process without food transfer as part of the move towards nutritional independence. In particular, fruits of *Saba comorensis*, which are a "top-ranking food item" that chimpanzees of the M group spend about 20% of their annual feeding time (Itoh, 2004), has a hard shell and is classified as "difficult food to process" (Nishida and Turner, 1996). These fruits are highly available from August to January (Itoh and Muramatsu, 2015), and although this period is limited, it is important for infants to be able to eat *S. comorensis* fruits by themselves to achieve nutritional independence. The observation that infant chimpanzees can process *S. comorensis* fruits well after 3-years-old concurs with the finding of a previous study on manual skills for processing fruits of *S. comorensis* (Corp and Byrne, 2002). In addition to this fruit, Nishida (1991) classified other "Major Food" and "Important Food" of chimpanzees of the M group. In this list, the piths of many species of terrestrial herbaceous vegetation (THV) (e.g., *Pennisetum purpureum*) are classified as food that is difficult

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for infants to process (Nishida and Turner, 1996), but are available almost year-round (Itoh et al., 2015). Thus, the ability of infants to eat THV piths year-round might contribute to nutritional independence.

Change points between 10−12-months-old were observed in ontogeny of feeding time (Fig. 2 B-1), feeding time on leaves (Fig. 2 B-2), and feeding time on difficult food with food transfer (Fig. 2 B-3). This period concurred with the completion of the eruption of deciduous teeth (Nissen and Riesen, 1945). Infants spent up to 15% of their time on feeding on solid foods at this change point. The current study did not investigate the period when infants start to eat, because of a lack of data on infants under 5-months-old. However, a previous study on chimpanzees in Mahale suggested that 5-months-old infant chimpanzees begin to eat for a short period of time (Hiraiwa-Hasegawa, 1990a). The subsequent completion of the eruption of deciduous teeth might allow infants to eat for relatively longer amounts of time. A further change point at 44-months-old was found in developmental changes in total feeding time. This period matched the time at which M1 reached functional occlusion (Machanda et al., 2015). At this change point, total feeding time ratio reached a maximum and was almost the same as that of adults (40% of daily activity time) (Hiraiwa-Hasegawa, 1990a). This result concurs with the previous studies in other field sites, such as Kibale (Smith et al., 2013) and Gombe (Lonsdorf et al., 2014). Additionally, total feeding time appeared to decrease just before 60-months-old. This phenomenon might be caused by the shortening of food processing time. However, it was not possible to conclude whether feeding time decreased just before 60-months-old in the current study because the 95% confidence interval was relatively wide at this time point.

M1 eruption is considered an important indicator of the weaning period in many primates (Smith, 1992),

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339 although not in apes (Robson and Wood, 2008). Smith et al. (2013) suggested that “M1 emergence in eastern
340 chimpanzees may relate to a key dietary transition around age 3”. The detailed behavioral data in this study
341 supported this suggestion. Therefore, M1 eruption in chimpanzees may be an index of the period when infants
342 move towards nutritional independence via a dietary transition.

343 The period when mothers stop nutritional investment (nursing) to the current infant and begin to invest in the
344 next infant (resume menstrual cycling and reconception) is a definition of the weaning age that assumes conflict
345 between mother and infant (Trivers, 1974). The main index of the weaning age in this assumption can be
346 calculated by subtracting gestational length from inter-birth interval (Lee et al., 1991). The weaning age of
347 chimpanzees using this index gives the same age (4−5-years-old) as the conventional cessation of nipple contact,
348 therefore, these two definitions and indexes have yet to be clearly distinguished from each other. However,
349 Emery Thompson et al. (2012) pointed out that the majority of mothers reduce their energetic investment to the
350 infant (including milk transfer, carrying on the infant, and so on) long before the resumption of menstrual
351 cycling and conception of the next offspring. The current study supported the prediction that infants move
352 towards nutritional independence at around 3-years-old. This period partially matches the period when mothers
353 reduce energetic investment (Emery Thompson et al., 2012), and these results highlight the temporal gap
354 between significant reduction in energetic investment to the infant and existing weaning age (4−5-years-old).
355 Bădescu et al. (2016) indicated this temporal gap between the nutritional independence of infants and the
356 reconception of chimpanzee mothers in Ngogo using fecal stable isotopes. Future studies should investigate the
357 actual amount of milk intake proportional to solid food intake by using stable isotopes at Mahale to reveal the

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358 relationship with the behavioral change point suggested by the current study.

359 This temporal gap between nutritional independence of infants and reconception of mothers has been
360 observed in other great apes. For example, orangutans have the longest inter-birth interval in primates, with a
361 weaning age based on cessation of nipple contact at 6−7-years-old (Humphrey, 2010; van Noordwijk and van
362 Schaik, 2005; van Noordwijk et al., 2013b). However, Sumatran orangutans (*Pongo abelii)* showed drastic
363 developmental changes in locomotive ability and started to feed separately from the mother at 3-years-old (van
364 Noordwijk and van Schaik, 2005). In addition, Bornean orangutans (*P. pygmaeus*) at 4−5-years-old significantly
365 reduced feeding time in the same patch as the mother. The ratio of food transfer during maternal feeding bouts
366 on difficult food also decreased considerably during this period (Jaeggi et al., 2008). Therefore, this period was
367 also regarded as weaning age (Jaeggi et al., 2010). In mountain gorillas (*Gorilla beringei beringei*), weaning
368 age, assessed by the complete cessation of nipple contact, matches the timing of conception of the next offspring
369 (3.4-years-old on average) (Stoinski et al., 2013). However, Watts (1985) reported that infants at around 2-years-
370 old can eat plant foods similar to that of older group members and that infants by the end of their third year can
371 eat all adult foods, including food difficult to process. These studies imply a temporal gap between nutritional
372 independence and conception of the next offspring in apes, as suggested for chimpanzees in this study.

373 In other non-ape primates, Tanaka (1992) suggested that mothers of Japanese macaques (*Macaca fuscata*)
374 reduce milk transfer at 6-months-old, and can resume menstrual cycling and reconceive at the same time when
375 in good nutritional condition. Sixty-five percent of the multiparous females give birth at an interval of one year
376 in a provisioned group (Koyama et al., 1992). Similarly, studies in patas monkeys (*Erythrocebus patas*)

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377 suggested that infants may move towards nutritional independence at 7-months-old (Chism, 1986), and that
378 twenty-five of 33 inter-birth intervals (approximately 75%) in wild are one-year long (Nakagawa et al., 2003).
379 Additionally, Borries et al. (2014) suggested that the earliest age at which orphans can survive without nursing
380 (the timing of nutritional independence) in wild Phayre's leaf monkeys (*Trachypithecus phayrei*) matches the
381 timing of conception of the next offspring. Twenty-five of 35 timings of reconception (about 70%) were shorter
382 than or consistent with the age of nutritional independence of infants (Borries et al., 2014). Furthermore,
383 Altmann (1980) researched wild yellow baboons (*Papio cynocephalus*), and suggested that infants at 12-
384 months-old were independent and perhaps could survive without the mother. This age matches the timing of
385 resumption of menstrual cycling of mothers (mean: 12−12.5, n = 20, range: 6−16), who take about four months
386 to conceive the next offspring (Altmann et al., 1977). Therefore, these studies of non-ape primates imply that
387 there is no or a very small gap between nutritional independence and the timing of conception of the next
388 offspring.

389 In chimpanzees in Mahale, the shortest inter-birth interval after surviving offspring (3.7 years; Emery
390 Thompson, 2013) minus gestation length (approximately 0.6 years; Tutin and McGinnis, 1981) gives a shortest
391 reconception period of about three years. However, this is very rare as the average inter-birth intervals following
392 surviving male and female infants in Mahale are 6.19 years (n = 9, sd = 1.03) and 5.18 years (n = 14, sd = 0.65),
393 respectively (Nakamura, 2015). Therefore, the large temporal gap between nutritional independence and
394 conception of the next offspring, may be a unique feature of the life history of chimpanzees (and great apes in
395 general). As aforementioned, this is rarely considered in chimpanzee studies because of the temporal accord

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between cessation of nipple contact and the timing of conception of the next offspring.

This study highlighted the large gap between nutritional independence and existing weaning age and clarified the unique feature of early weaning in humans (Humphrey, 2010). The results showed that infants significantly changed their feeding behavior at 3-years-old, long before cessation of nipple contact and the timing of conception of the next offspring. Furthermore, results supported the suggestion by Emery Thompson et al. (2012) that inter-birth interval in chimpanzees is much longer than in other primates as females need to sustain a positive energy balance and recover their physical condition after significant reduction of milk production, rather than the direct expense of milk production itself. Future behavioral studies should investigate the meaning of this gap from the stand point of infants, which might continue receiving some investments from the mother other than maternal milk (e.g., sharing a bed, learning social behaviors, or sharing a food patch) (Matsumoto and Hayaki, 2015; Nakamura et al., 2014). In contrast to chimpanzees and other great apes, a unique feature of humans is that mothers may start to invest in the next offspring “before” nutritional independence of infants (Bogin, 1999). This study highlighted the importance of specially prepared complementary foods for human infants (van Noordwijk et al., 2013a) and/or provisioning and cooperative breeding by allomothers (Hrdy, 2016) for human mothers to conceive the next offspring much earlier than great apes do.

Acknowledgements

I thank the Tanzania Commission for Science and Technology (COSTECH), Tanzania Wildlife Research Institute (TAWIRI), Tanzania National Parks (TANAPA), and the Mahale Mountains Wildlife Research Centre

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(MMWRC) for permission to conduct this research at Mahale; local assistants of Mahale Mountains Chimpanzee Research Project (MMCRP), for their daily help in the field; and Julius Keyyu, for logistic support. I am deeply grateful to Naofumi Nakagawa, Michio Nakamura, Juichi Yamagiwa, Eiji Inoue, and colleagues in the Laboratory of Human Evolution Studies at Kyoto University for meaningful discussion and meticulous comments on the earlier version of the manuscript. I greatly thank research colleagues of MMCRP for generous support at the field site and insightful comments on this study. I appreciate the support and encouragement from Ichiro Tayasu and colleagues of the Research Institute for Humanity and Nature. This research was financially supported by The Ministry of Education, Culture, Sports, Science, and Technology (MEXT) KAKENHI (Grant number 19255008, 19107007, 24255010); and Japan Society for the Promotion of Science (JSPS) KAKENHI (Grant number 14J00562, 16J03218). I thank David Watts and two anonymous reviewers for providing constructive comments and edits on the manuscript.

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Literature Cited

Agetsuma, N. (2001). Relation between age–sex classes and dietary selection of wild Japanese monkeys. *Ecological. Research*, 16, 759−763.

Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour*, 49, 227−267.

Altmann, J. (1980). *Baboon Mothers and Infants*. Cambridge, MA: Harvard University Press.

Altmann, J., Altmann, S.A., Hausfater, G., & McCuskey, S.A. (1977). Life history of yellow baboons: Physical development, reproductive parameters, and infant mortality. *Primates*, 18, 315−330.

Austin, C., Smith, T. M., Bradman, A., Hinde, K., Joannes-Boyau, R., Bishop, D., Hare, D. J., Doble, P., Eskenazi, B., & Arora, M. (2013). Barium distributions in teeth reveal early-life dietary transitions in primates. *Nature*, 498, 216−219.

Bădescu, I., Katzenberg, M. A., Watts, D. P., & Sellen, D. W. (2017). A novel fecal stable isotope approach to determine the timing of age-related feeding transitions in wild infant chimpanzees. *American Journal of Physical Anthropology*, 162, 285−299.

Boesch, C., Bole, C., Eckhardt, N., & Boesch, H. (2010). Altruism in forest chimpanzees: the case of adoption. *PLoS One*, 5, e8901.

Bogin, B. (1999). Evolutionary perspective on human growth. *Annual Review of Anthropology*, 28, 109−153.

Borries, C., Lu, A., Ossi-Lupo, K., Larney, E., Koenig, A. (2014). The meaning of weaning in wild Phayre's leaf monkeys: Last nipple contact, survival, and independence. *American Journal of Physical Anthropology*, 154, 291−301.

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京都大学学術情報リポジトリ KURENAI 紅 Kyoto University Research Information Repository

447 Bronstrom, G. (2013). glmmML: generalized linear models with clustering. R package version 1.0.

448 Burnham, K. P., & Anderson, D. R. (Eds.) (2002). Information and likelihood theory: a basis for model
449 selection and inference. In: *Model Selection and Multimodel Inference*. New York: Springer
450 Science+Business Media,.

451 Burnham, K. P., & Anderson, D. R. (2004). Multimodel inference: understanding AIC and BIC in model
452 selection. *Sociological Methods & Research*, 33, 261−304.

453 Chism, J. (1986). Development and mother-infant relations among captive patas monkeys. *International*
454 *Journal of Primatology*, 7, 49−81.

455 Corp, N., & Byrne, R. W. (2002). The ontogeny of manual skill in wild chimpanzees: evidence from feeding
456 on the fruit of *Saba florida*. *Behaviour,* 139, 137−168.

457 Crawley, M. J. (2005). *Statistics: an introduction using R*. Chichester: John Wiley & Sons Ltd.

458 Duda, P., & Zrzavý, J. (2013). Evolution of life history and behavior in Hominidae: Towards phylogenetic
459 reconstruction of the chimpanzee–human last common ancestor. *Journal of Human Evolution*, 65,
460 424−446.

461 Emery Thompson, M. (2013). Reproductive ecology of female chimpanzees. *American Journal of*
462 *Primatology*, 75, 222−237.

463 Emery Thompson, M., Jones, J. H., Pusey, A. E., Brewer-Marsden, S., Goodall, J., Marsden, D., Matsuzawa,
464 T., Nishida, T., Reynolds, V., Sugiyama, Y., & Wrangham, R. W. (2007). Aging and fertility patterns in
465 wild chimpanzees provide insights into the evolution of menopause. *Current Biology*, 17, 2150−2156.

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466 Emery Thompson, M., Muller, M. N., & Wrangham, R. W. (2012). The energetics of lactation and the return
467 to fecundity in wild chimpanzees. *Behavioural Ecology*, 23, 1234–1241.
468 Fahy, G. E., Richards, M. P., Fuller, B. T., Deschner, T., Hublin, J. J., & Boesch, C. (2014). Stable nitrogen
469 isotope analysis of dentine serial sections elucidate sex differences in weaning patterns of wild
470 chimpanzees (*Pan troglodytes*). *American Journal of Physical Anthropology*, 153, 635–642.
471 Galef, B. (2009). Maternal influences on offspring food preferences and feeding behaviors in mammals. In:
472 Maestripieri, D., Mateo, J. M. (Eds.), *Maternal effects in mammals*. Chicago, IL: University of Chicago
473 Press, pp. 159−181.
474 Goodall, J. (1986). *The chimpanzees of Gombe: Patterns of behavior*. Boston, MA: Belknap Press of Harvard
475 University Press.
476 Hamada, Y., & Udono, T. (2002). Longitudinal analysis of length growth in the chimpanzee (*Pan troglodytes*).
477 *American Journal of Physical Anthropology*, 118, 268−284.
478 Hayaki, H. (1988). Association partners of young chimpanzees in the Mahale Mountains National Park,
479 Tanzania. *Primates*, 29, 147−161.
480 Hinde, K., & Milligan, L. A. (2011). Primate milk: proximate mechanisms and ultimate perspectives.
481 *Evolutionary Anthropology* ,20, 9−23.
482 Hiraiwa-Hasegawa, M. (1990a). A note on the ontogeny of feeding. In: Nishida, T. (Ed.), *The chimpanzees of*
483 *the Mahale mountains: Sexual and life history strategies*. Tokyo: Tokyo University Press, pp. 277−283.

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京都大学学術情報リポジトリ KURENAI 紅 Kyoto University Research Information Repository

Hiraiwa-Hasegawa, M. (1990b). Maternal investment before weaning. In: Nishida, T. (Ed.), *The chimpanzees of the Mahale mountains: Sexual and life history strategies*. Tokyo: Tokyo University Press, pp. 257−266.

Hiraiwa-Hasegawa, M. (1990c). The role of food sharing between mother and infant in the ontogeny of feeding behavior. In: Nishida, T. (Ed.), *The chimpanzees of the Mahale mountains: Sexual and life history strategies*. Tokyo: Tokyo University Press, pp. 267−275.

Hiraiwa-Hasegawa, M., Hasegawa, T., & Nishida, T. (1984). Demographic study of a large-sized unit-group of chimpanzees in the Mahale Mountains, Tanzania: A preliminary report. *Primates*, 25, 401−413.

Hrdy, S. B. (2016). Variable postpartum responsiveness among humans and other primates with "cooperative breeding": A comparative and evolutionary perspective. *Hormones and Behavior*, 77, 272−283.

Humphrey, L. T. (2010). Weaning behaviour in human evolution. *Seminars in Cell And Developmental Biology*, 21, 453-461.

Itoh, N. (2004). Plant phenology and chimpanzee fission–fusion grouping system in Mahale Mountains National Park. Ph.D. Dissertation, Kyoto University.

Itoh, N. (2015). Climate and climatological trends in the Kasoje forest. In: Nakamura, M., Hosaka, K., Itoh, N., Zamma, K. (Eds.), *Mahale Chimpanzees: 50 years of research*. Cambridge: Cambridge University Press, pp. 143−149.

Itoh, N., & Muramatsu, D. (2015). Patterns and trends in fruiting phenology: some important implications for chimpanzee diet. In: Nakamura, M., Hosaka, K., Itoh, N., Zamma, K. (Eds.), *Mahale Chimpanzees: 50 Years of Research*. Cambridge: Cambridge University Press, pp. 174−194.

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京都大学学術情報リポジトリ KURENAI 紅 Kyoto University Research Information Repository

503 Itoh, N., Nakamura, M., 2015a. Diet and feeding behavior. In: Nakamura, M., Hosaka, K., Itoh, N., Zamma,
504 K. (Eds.), *Mahale Chimpanzees: 50 Years of Research*. Cambridge: Cambridge University Press, pp.
505 227−245.
506 Itoh, N., & Nakamura, M. (2015b). Mahale flora: its historical background and long-term changes. In:
507 Nakamura, M., Hosaka, K., Itoh, N., Zamma, K. (Eds.), *Mahale Chimpanzees: 50 Years of Research*.
508 Cambridge: Cambridge University Press, pp. 150−173.
509 Itoh, N., Zamma, K., Matsumoto, T., Nishie, H., & Nakamura, M. (2015). Appendix II Dietary list. In:
510 Nakamura, M., Hosaka, K., Itoh, N., Zamma, K. (Eds.), *Mahale Chimpanzees: 50 Years of Research*.
511 Cambridge: Cambridge University Press, pp. 717–739.
512 Jaeggi, A. V., van Noordwijk, M. A., & van Schaik, C. P. (2008). Begging for information: mother-offspring
513 food sharing among wild Bornean orangutans. *American Journal of Primatology*, 70, 533−541.
514 Jaeggi, A. V., Dunkel, L. P., van Noordwijk, M. A., Wich, S. A., Sura, A. A. L., & van Schaik, C. P. (2010).
515 Social learning of diet and foraging skills by wild immature Bornean orangutans: implications for culture.
516 *American Journal of Primatology*, 72, 62−71.
517 Koyama, N., Takahata, Y., Huffman, M. A., Norikoshi, K., & Suzuki, H. (1992). Reproductive parameters of
518 female Japanese macaques: Thirty years data from the Arashiyama troops, Japan. *Primates*, 33, 33−47.
519 Langer, P. (2008). The phases of maternal investment in eutherian mammals. *Zoology*, 111,
520 148−162.

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https://repository.kulib.kyoto-u.ac.jp
京都大学学術情報リポジトリ KURENAI 紅 Kyoto University Research Information Repository

521 Lee, P. C., Majluf, P., and Gordon, I. J. (1991). Growth, weaning and maternal investment from a comparative
522 perspective. *Journal of Zoology*, 225, 99−114.
523 Lonsdorf, E. V., Markham, A. C., Heintz, M. R., Anderson, K. E., Ciuk, D. J., Goodall, J., & Murray, C. M.
524 (2014). Sex differences in wild chimpanzee behavior emerge during infancy. *PLoS One*, 9, e99099.
525 Machanda, Z., Brazeau, N. F., Bernard, A. B., Donovan, R. M., Papakyrikos, A. M., Wrangham, R., & Smith,
526 T.M. (2015). Dental eruption in East African wild chimpanzees. *Journal of Human Evolution*, 82,
527 137−144.
528 Maindonald, J. H., & Braun, W. J. (2015). Data Analysis and Graphics Data and Functions. R package version
529 1.22.
530 Matsumoto, T., & Hayaki, H. (2015). Development and growth: with special reference to mother–infant
531 relationships. In: Nakamura, M., Hosaka, K., Itoh, N., Zamma, K. (Eds.), *Mahale Chimpanzees: 50 Years*
532 *of Research*. Cambridge: Cambridge University Press, pp. 313–325.
533 Matsumoto, T., Itoh, N., Inoue, S., & Nakamura, M. (2016). An observation of a severely disabled infant
534 chimpanzee in the wild and her interactions with her mother. *Primates*, 57, 3−7.
535 Meehan, C. L., & Crittenden, A. N. (2016). *Childhood: Origins, Evolution, and Implications*. Albuquerque:
536 University of New Mexico Press.
537 Nakagawa, N., Ohsawa, H., & Muroyama, Y. (2003). Life-history parameters of a wild group of West African
538 patas monkeys (*Erythrocebus patas patas*). *Primates*, 44, 281−290.

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https://repository.kulib.kyoto-u.ac.jp
京都大学学術情報リポジトリ KURENAI 紅 Kyoto University Research Information Repository

539 Nakamura, M. (2015). Demography of the M group. In: Nakamura, M., Hosaka, K., Itoh, N., Zamma, K.
540 (Eds.), *Mahale Chimpanzees: 50 Years of Research*. Cambridge: Cambridge University Press, pp. 82−93.
541 Nakamura, M., Corp, N., Fujimoto, M., Fujita, S., Hanamura, S., Hayaki, H., Hosaka, K., Huffman, M. A.,
542 Inaba, A., Inoue, E., Itoh, N., Kutsukake, N., Kiyono-Fuse, M., Kooriyama, T., Marchant, L. F.,
543 Matsumoto-Oda, A., Matsusaka, T., McGrew, W. C., Mitani, J. C., Nishie, H., Norikoshi, K., Sakamaki, T.,
544 Shimada, M., Turner, L. A., Wakibara, J. V., & Zamma, K. (2013). Ranging behavior of Mahale
545 chimpanzees: a 16 year study. *Primates*, 54, 171−182.
546 Nakamura, M., Hayaki, H., Hosaka, K., Itoh, N., & Zamma, K. (2014). Orphaned male Chimpanzees die
547 young even after weaning. *American Journal of Physical Anthropology*, 153, 139−143.
548 Nakamura, M., & Hosaka, K. (2015). Orphans and allomothering. In: Nakamura, M., Hosaka, K., Itoh, N.,
549 Zamma, K. (Eds.), *Mahale Chimpanzees: 50 Years of Research*. Cambridge: Cambridge University Press,
550 pp. 421−432.
551 Nakamura, M., & Itoh, N. (2015). Overview of the field site: Mahale Mountains and their surroundings. In:
552 Nakamura, M., Hosaka, K., Itoh, N., Zamma, K. (Eds.), *Mahale Chimpanzees: 50 Years of Research*.
553 Cambridge: Cambridge University Press, pp. 7−20.
554 Nishida, T. (1991). Primate gastronomy: Cultural food preferences in nonhuman primates and origins of
555 cuisine. In: Friedman, M. I., Tordoff, M. G., Kare, M. R. (Eds.), *Chemical Senses, Vol. 4: Appetite and*
556 *Nutrition*. New York: Marcel Dekker, pp. 195−209.
557 Nishida, T. (1994). *Thirty-six Stories of Wild Chimpanzees*. Tokyo: Kinokuniya-shoten (in Japanese).

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https://repository.kulib.kyoto-u.ac.jp
京都大学学術情報リポジトリ KURENAI 紅 Kyoto University Research Information Repository

558 Nishida, T. (2012). *Chimpanzees of the lakeshore: natural history and culture at Mahale*. Cambridge:
559 Cambridge University Press.
560 Nishida, T., & Hiraiwa, M. (1982). Natural history of a tool-using behavior by wild chimpanzees in feeding
561 upon wood-boring ants. *Journal of Human Evolution*, 11, 73−99.
562 Nishida, T., Takasaki, H., & Takahata, Y. (1990). Demography and reproductive profiles. In: Nishida, T. (Ed.),
563 The chimpanzees of the Mahale mountains: Sexual and life history strategies. Tokyo: Tokyo University
564 Press, pp. 63−97.
565 Nishida, T., & Turner, L.A. (1996). Food transfer between mother and infant chimpanzees of the Mahale
566 Mountains National Park, Tanzania. *International Journal of Primatology*, 17, 947−968.
567 Nishie, H. (2011). Natural history of *Camponotus* ant-fishing by the M group chimpanzees at the Mahale
568 Mountains National Park, Tanzania. *Primates*, 52, 329−342.
569 Nissen, H. W. & Riesen, A.H. (1945). The deciduous dentition of chimpanzee. *Growth*, 9, e274.
570 Norikoshi, K. (2002). Vegetation of Kasoje research area and ranging pattern: Changes during 20 years before
571 and after the establishment of national park. In: Nishida, T., Uehara, S., Kawanaka, K. (Eds.), *The Mahale*
572 *Chimpanzees: 37 years of Panthropology*, pp. 101−288 (in Japanese).
573 Nowell, A. A., & Fletcher, A. W. (2008). The development of feeding behaviour in wild western lowland
574 gorillas (*Gorilla gorilla gorilla*). *Behaviour*, 145, 171−193.
575 R Core Team (2015). R: A language and environment for statistical computing. R Foundation for Statistical
576 Computing, Vienna.

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京都大学学術情報リポジトリ KURENAI 紅 Kyoto University Research Information Repository

577 Reitsema, L. J. (2012). Introducing fecal stable isotope analysis in primate weaning studies. *American Journal*
578 *of Primatology*, 74, 926−939.
579 Robson, S. L., & Wood, B. (2008). Hominin life history: reconstruction and evolution. *Journal of Anatomy*,
580 212, 394−425.
581 Sellen, D. W. (2001). Comparison of infant feeding patterns reported for nonindustrial populations with
582 current recommendations. *Journal of Nutrition*, 131, 2707−2715.
583 Sellen, D. W. (2007). Evolution of infant and young child feeding: implications for contemporary public
584 health. *Annual Review of Nutrition*, 27, 123−148.
585 Silk, J. B. (1978). Patterns of food sharing among mother and infant chimpanzees at Gombe National Park,
586 Tanzania. *Folia Primatologica*, 29, 129−141.
587 Smith, B. H. (1992). Life history and the evolution of human maturation. *Evolutionary Anthropology*, 1,
588 134−142.
589 Smith, T. M., Machanda, Z., Bernard, A. B., Donovan, R. M., Papakyrikos, A. M., Muller, M. N., &
590 Wrangham, R. (2013). First molar eruption, weaning, and life history in living wild chimpanzees.
591 *Proceedings of the National Academy of Sciences USA*, 110, 2787−2791.
592 Stoinski, T. S., Perdue, B., Breuer, T., & Hoff, M. P. (2013). Variability in the developmental life history of the
593 genus *Gorilla*. *American Journal of Physical Anthropology*, 152, 165−172.
594 Takemoto, H. (2003). Phytochemical determination for leaf food choice by wild chimpanzees in Guinea,
595 Bossou. *Journal of Chemical Ecology*, 29, 2551−2573.

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京都大学学術情報リポジトリ KURENAI 紅 Kyoto University Research Information Repository

596 Tanaka, I. (1992). Three phases of lactation in free-ranging Japanese macaques. *Animal Behaviour*, 44,
597 129−139.
598 Taniguchi, H. (2015). How the physical properties of food influence its selection by infant Japanese macaques
599 inhabiting a snow-covered area. *American Journal of Primatology*, 77, 285−295.
600 Tarnaud, L. (2004). Ontogeny of feeding behavior of *Eulemur fulvus* in the dry forest of Mayotte.
601 *International Journal of Primatology*, 25, 803−824.
602 Trivers, R. L. (1974). Parent-offspring conflict. *American Zoologist*, 14, 249−264.
603 Tsutaya, T., Shimomi, A., Fujisawa, S., Katayama, K., & Yoneda, M. (2016). Isotopic evidence of
604 breastfeeding and weaning practices in a hunter–gatherer population during the Late/Final
605 Jomon period in eastern Japan. *Journal of Archaeological Science*, 76, 70−78.
606 Tsutaya, T., & Yoneda, M. (2013). Quantitative reconstruction of weaning ages in archaeological
607 human populations using bone collagen nitrogen isotope ratios and approximate Bayesian
608 computation. *PLoS One*, 8, e72327.
609 Tutin, C. E., & McGinnis, P. R. (1981). Chimpanzee reproduction in the wild. In: C. Graham (Ed.),
610 *Reproductive biology of the great apes: Comparative and biomedical perspectives*. Cambridge: Academic
611 Press, pp. 202−212.
612 van Noordwijk, M. A., & van Schaik, C. P. (2005). Development of ecological competence in Sumatran
613 orangutans. *American Journal of Physical Anthropology*, 127, 79−94.

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van Noordwijk, M. A., Kuzawa, C. W., & van Schaik, C. P. (2013a). The evolution of the patterning of human lactation: a comparative perspective. *Evolutionary Anthropology*, 22, 202−212.

van Noordwijk, M. A., Willems, E. P., Atmoko, S. S. U., Kuzawa, C. W., & van Schaik, C. P. (2013b). Multi-year lactation and its consequences in Bornean orangutans (*Pongo pygmaeus wurmbii*). *Behavioral Ecology and Sociobiology*, 67, 805−814.

Watts, D. P. (1985). Observations on the ontogeny of feeding-behavior in mountain gorillas (*Gorilla gorilla beringei*). *American Journal of Primatology*, 8, 1−10.

Wobber, V., & Hare, B. (2011). Psychological health of orphan bonobos and chimpanzees in African sanctuaries. *PLoS One*, 6, e17147.

Wood, S., & Scheipl, F. (2015). Generalized additive mixed models using mgcv and lme4. R package version 0. 2−3.

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1 **Table 1. Individuals in this study**

Name[1]	Abbreviation	No. of scan points	No. of observation days	Age in months[3]	Sex	Mother
Asahi	AH	1115	7	14–47	♀	Multipara
Ayu	AY	2446	11	9–37	♀	Multipara
Cissy	CI	1985	9	36–58	♀	Multipara
-	CY14	175	2	13	♂	Multipara
Figaro	FG	2781	14	12–42	♂	Multipara
Iris	IR	1174	7	18–42	♀	Multipara
-	JJ13	257	1	23	♀	Primipara
Omali	OL	1036	8	6–28	♂	Primipara
-	PF14	304	2	14	♂	Primipara
-	QA13	710	3	29–31	♀	Multipara
Quilt	QL	266	1	50	♀	Multipara
Shinji	SJ	1518	8	13–43	♂	Multipara
Teto	TO	2573	12	34–59	♀	Multipara
-	TZ09[2]	2309	10	16–23	♀	Multipara
Upepo	UP	3193	16	9–37	♀	Primipara
Xyla	XL	1555	7	1–32	♀	Primipara
Zorufa	ZF	374	2	44–48	♀	Multipara

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-	ZL13	228	1	26	♂	Multipara

[1] Researchers at Mahale do not name infants under 3-years-old because of high infant mortality, therefore, I used the mothers' abbreviation, plus the latter two digits of the birth years to label unnamed infants.

[2] TZ09 died before 3-years-old.

[3] For individuals with multiple datasets from different seasons (years), the age range of the individual is shown.

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Table 2. Parameter estimates, AIC, and ΔAIC values for models

Order	AIC (ΔAIC)	P value	Parameter estimates		
		Age in months[1]	Intercept	Feeding time ratio of mother	Traveling time ratio of mother
(A) Number of Nipple contact					
1	**774.2 (0.0)**	**<0.001**	**-2.9±0.2**	**-0.9±0.3**	**-0.6±0.4**
2	774.6 (0.4)	<0.001	-3.0±0.2	-0.9±0.3	—
(B-1) Number of Feeding					
1	**1128.1 (0.0)**	**<0.001**	**-2.2±0.1**	**2.4±0.1**	**-0.4±0.2**
2	1129.3 (1.2)	<0.001	-2.3±0.1	2.4±0.1	—
(B-2) Number of Feeding on leaves					
1	**752.8 (0.0)**	**<0.001**	**-4.2±0.2**	**9.9±0.8**	**-2.7±0.7**
2	754.6 (1.8)	<0.001	-2.3±0.1	2.4±0.1	—
(B-3) Number of food transfer in feeding on difficult food					
1	**983.6 (0.0)**	**<0.001**	**-1.3±0.5**	**4.6±1.5**	**—**
2	985.4 (1.8)	<0.001	-1.4±0.5	4.6±1.5	0.1±1.1

The best model is in bold.

[1]As 'Age in months' is smoothed for modeling, the coefficient could not be evaluated.

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Figure 1

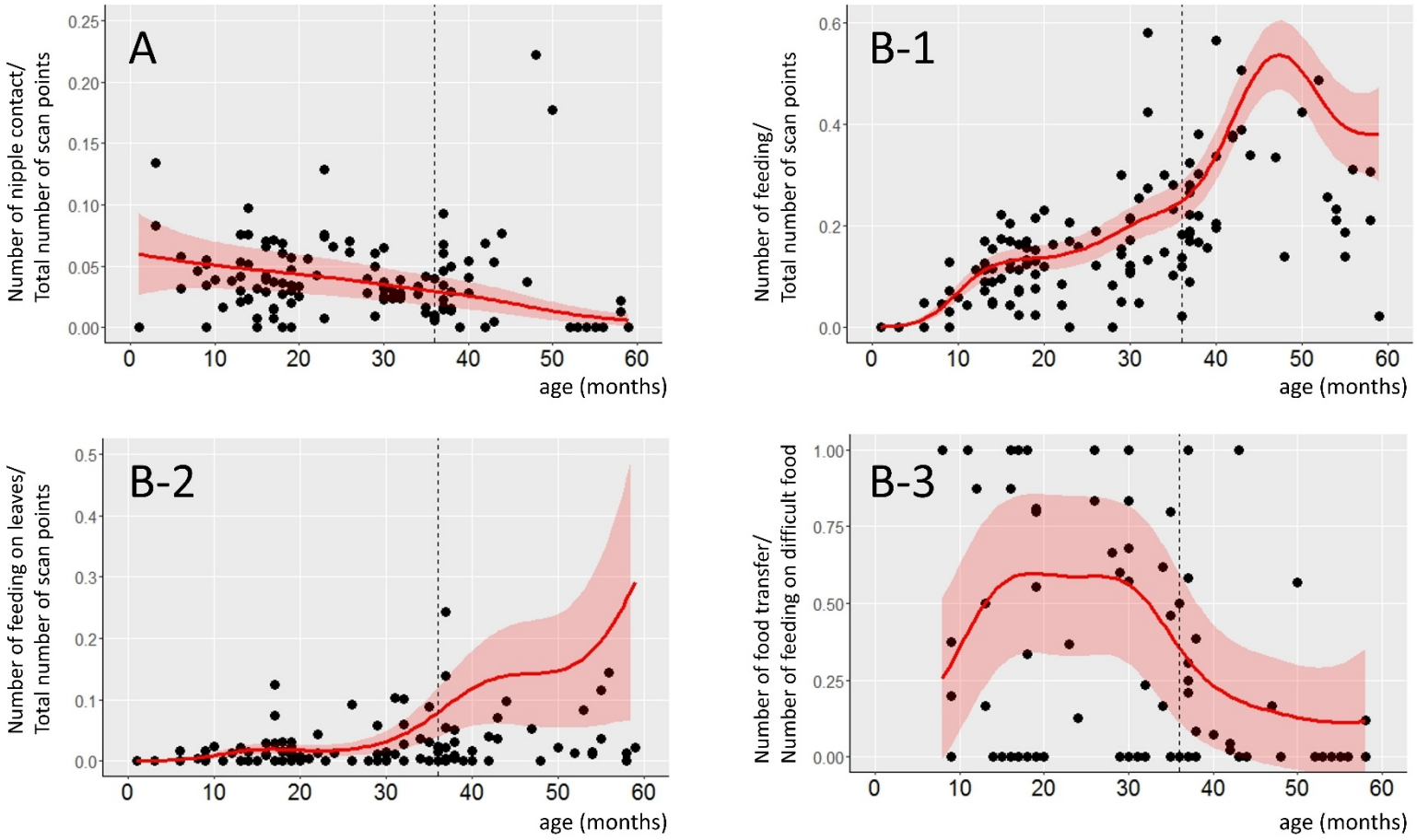

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Figure 2